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PAPERS.

26. A Study of the Remarkable Tortoise, *Testudo loveridgii* Blgr., and the Morphogeny of the Chelonian Carapace. By Joan B. Procter, F.Z.S.

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(Plates I.–III.*; Text-figures 1–21; and Table.)

Index.

Introduction.

In the preparation of the present paper, I am indebted to many persons for help and various courtesies. My especial thanks are due to Mr. A. Loveridge, for his generosity in allowing

* For explanation of the Plates, see p. 526.

me to use the whole of his valuable collection for dissection and general study. Also to Sir John Bland-Sutton, for his gift of X-ray plates of the types and young, and facility to study the tortoises themselves beneath the fluorescent screen at Middlesex Hospital at a time when no specimens could be spared for dissection; and also to Mr. R. H. Burne, of the Royal College of Surgeons, for investigating the structure of the denticulated jaw, and the ribs, and for making slides of them.

The purport of the present work is to furnish a detailed description of this extraordinary Soft Tortoise, based upon the large series of specimens which have passed through my hands; especially of the peculiarly interesting structure of the bony carapace and its development, compared with cases of fenestration in *Testudo* and other groups. The recently discovered young is also described in comparison with the adult, and various notes on the habits of living specimens by Mr. Loveridge are appended.

General Account.

Material and history.

In 1920, when Mr. G. A. Boulenger first examined this tortoise, then new to science, there were no specimens available for the making of a skeleton. The carapace, which feels soft and springy, was examined by cutting a flap in the abdominal shields, removing the viscera, and holding the animal against the light. When this is done, no bony matter of any kind can be detected; the carapace is seemingly translucent without ribs or costal plates: it was therefore described as boneless. The view obtained in this way is deceptive, as it is limited to the region of the second and third costal and vertebral shields on account of the restrictions of the fenestra in the plastron through which it is viewed; the shadows of the reduced costal plates, which are there, are entirely obscured by the black markings in the epidermal shields.

The young specimen described in his note*, although agreeing in almost every particular with the type, excepting its convexity, was an anomalous specimen, not the young of *loveridgii*. In 1921, Mr. Loveridge sent a Kaffir on an expedition to hunt for further material, and the true young was found in the type-locality This has a depressed carapace, but does not resemble the adult in general appearance. Since then further expeditions have succeeded in capturing more specimens, both adult, young, and half-grown, so that at one time and another I have been able to examine twenty-three spirit specimens, besides two specimens at present living in the Zoological Gardens. It has also been possible to prepare skeletons both of adult and young, and to make dissections.

After examining this new material, Mr. Boulenger agrees

* Boulenger, C. R. Acad. Sci., Paris, t. 170, p. 264 (1920).

with me in my three principal amendments to his original description:—

1. That the type-specimens are fully adult.

2. That the adults have bony neural and costal plates present to a certain degree.

3. That the young has a more or less depressed carapace.

Characteristics.

Testudo loveridgii is already well known as the Soft-shelled Tortoise with the flat carapace, both these characteristics being entirely foreign to *Testudo* as previously defined.

In general appearance it looks as if it had been crushed in youth and had only survived by a miracle. When taken in the hand alive it has a boneless feeling which is uncanny; both carapace and plastron react to pressure on the abdominal region with a springy motion, and the animal is able to inflate itself to a slight degree.

Mr. Boulenger pointed out in his note that in the case of the plastron this softness is due to an enormous diamond-shaped fenestra, usually met with in the newly-hatched or very young of other species. The viscera thus exposed are protected by extremely thick, soft, dermis of a very tough nature.

The true structure of the carapace was revealed by X-rays quite accidentally, my original object being to compare the supposedly boneless adult with the young, in which the ribs show normal development. When viewed through the fluorescent screen, the adults presented an extraordinary appearance, the ribless vertebræ and more or less normal limb-girdles being overlaid by a bony network, intimately correlated with the net of sutures between the epidermal shields, and formed by the partial development of the neural and costal plates which had been apparently wanting, and which in other species compose the solid bony carapace (*vide* Pls. II. & III.). The significance of this bony network only became clear after considerable study of the X-ray plate taken at the time. The skeleton subsequently prepared corroborated every detail revealed in this plate, and also showed that the vertebræ are very remarkable in form. The animal is further remarkable in possessing what appear to be teeth, acrodont in type and similar to those met with in Agamoid lizards. Their regularity renders them quite unlike the serrations met with in some tortoises. The horny sheaths of the alveolar ridges are similarly denticulated.

In the detailed description which follows, these structures will be dealt with at greater length.

The species is still in a state of great instability, for apart from the immense range of variation to which it is subject, many abnormalities occur, such as the presence of horny shields proper to the more primitive Chelonians.

Affinities.

Testudo loveridgii is undoubtedly closely related to *T. tornieri* Sieb. Even before the skeletal characters were known, when the former was thought to be without a bony carapace, it was recognized as being nearer to the latter species than to any other; in fact, Mr. Loveridge took his first specimens to be *tornieri*. Comparison of their skeletons show that they are similar in structure.

Briefly, they are probably both derived from the *geometrica* group, *loveridgii* being one step further removed than *tornieri*.

T. tornieri differs from *T. loveridgii* in that the carapace is not quite so depressed. The bony plates beneath are rather more developed, and slightly different in arrangement. It has a ninth pair of well-developed costal plates, and the whole animal is relatively much longer, being about half as broad as long instead of two-thirds.

The supracaudal shield is also entire, instead of divided as is usually the case in *loveridgii*. It possesses, however, all the special peculiarities of *loveridgii*, including the deficient ribs, and fenestrated carapace and plastron, which produces a soft-shelled condition. It also appears, from its photographs, to have both jaws regularly denticulated.

Siebenrock's two specimens from Bussisi and Lindi are described as having soft shells, but he considered the condition of the carapace which he dissected away in one individual to be pathological (1904). The finding of a third specimen by Lönnberg at Njoro (1911) and the recent discovery of *loveridgii*, however, prove that it is merely physiological.

Habitat and habits.

T. loveridgii is found in the arid rocky country round Dodomo and Tabora in Tanganyika Territory. Its distribution seems to be restricted to rocky kopjes where great boulders of grey granite are scattered; the characteristic vegetation is of the thorn-bush type; capers are also numerous.

The tortoise is good at climbing up the face of the rock, and turns over easily after falling on its back. It can only be dislodged from crevices with difficulty, as it is able to inflate itself to a certain degree, and thus wedge itself firmly, using its legs as struts. It is also able to squeeze itself beneath stones, on account of the springy structure of its carapace.

It is probable that it lays a single oval egg (about 35 mm. long and 23 mm. in diameter), as such a one was recently dug up by Mr. Loveridge in the enclosure in which several females were penned. The embryo extracted from this egg is almost at the point of hatching, and I have little doubt that it is *loveridgii*; but it is not possible to be certain, as females of *T. pardalis* and *Cinixys belliana* were also in the pen, and tortoise-embryos are very similar to one another, and at this stage the more striking characteristics of *loveridgii* are not manifest.

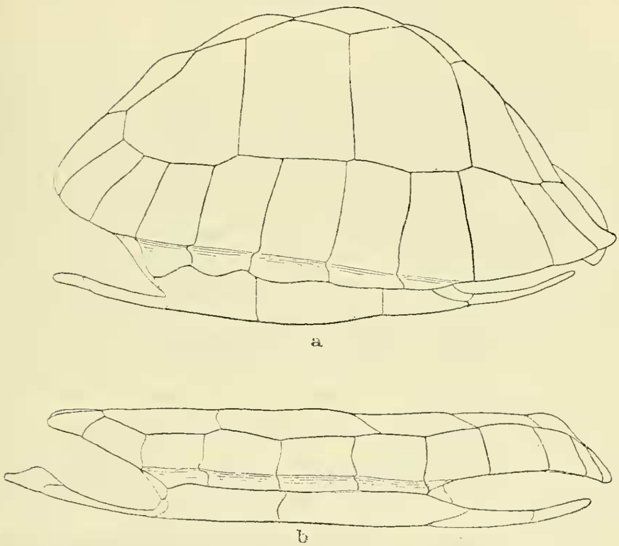
Further particulars as to habits will be found in the notes by Mr. Loveridge appended to this paper.

External Characters.

Shape and proportions.

The carapace of the adult is from three-quarters to four-fifths broad as long (actually 71 to 83 per cent.), excessively depressed, either flat or concave in the vertebral region; depth usually about one-fifth of the length. In text-fig. 1 (*q. v.*) the depressed carapace of *loveridgii* is compared with that of the normal *ibera*. Marginal region turning downwards and outwards abruptly, excepting the anterior border, which remains flat; marginals four to eight sometimes perpendicular. Sides straight, either

Text-figure 1.



Carapace of a normal Tortoise, *T. ibera* (a), compared with that of *T. loveridgii* (b).

parallel or oblique; anterior edge of shell straight or forming a slightly inverted curve, feebly serrated; posterior border rounded or obtusely pointed, also slightly serrated. Sometimes the greatest width is in the pectoral and sometimes in the pelvic region, but in the majority it is equal at and between these two positions. This depends upon the oblique or parallel trend of the sides of the carapace. In the table of measurements the breadth is always taken at mid-carapace.

The young are as broad as long and about one-third deep as long, and the carapace is uniformly convex and cordiform in outline. With growth these proportions change, the tortoise becoming narrower and more depressed. In order to show the precise nature of this change in form, the specimens in the appended table are graded according to age; the regular fall of the percentage values for breadth and depth are thus obvious, and could be well expressed by graphs.

In both adults and young the dimension of depth does not properly apply to the carapace *s. str.*, but to the thickness of the entire animal.

The plastron is large and projects beyond the carapace in front and falls short of it behind; fore-lobe truncate, hind-lobe deeply cleft, the two about equal in length and nicely shaped around the limbs; bridge very variable in width, usually about once and a half the length of either lobe. In the young the breadth of the entire plastron is greater in proportion.

Coloration.

The system of markings is similar to that met with in the *geometrica* group; the pattern, however, does not form regular stars, on account of the excentric positions of the areolars. These surfaces are reddish brown or rust-colour, black and pale horn-coloured bands radiating from them to the shield-edge; the rays are sometimes very strongly marked and regular, sometimes one colour predominating and sometimes the other, according to whether the black rays are broad or narrow, strongly marked or indistinct (*vide* Pl. I.). In the young the dark pigment is irregularly massed around each areolar. Each shield has its characteristic design, according to its contours; in well marked specimens that of the fifth vertebral resembles a rising sun, as depicted in decorative art; those on the marginals, the aster-pattern of old blue china.

On the plastron the system is the same, but the yellow or horn-colour greatly predominates, partly owing to the larger areolars and partly to the fact that the black rays do not always reach to the shield-edge.

The head and limbs are brownish or yellowish, sometimes indistinctly mottled.

Owing to the burrowing proclivities of these tortoises, the live specimens usually have their beautiful markings entirely obscured by dirt, which lodges in the deep concentric striations of the shields.

Mr. Loveridge notes that the specimens from Tabora are lighter in colour than those from Dodoma.

Head.

Head moderate; tympanum as large as or larger than eye: frontal usually broken up into four shields; præfrontal large, subcordiform, divided in one specimen; a pair of large supra-

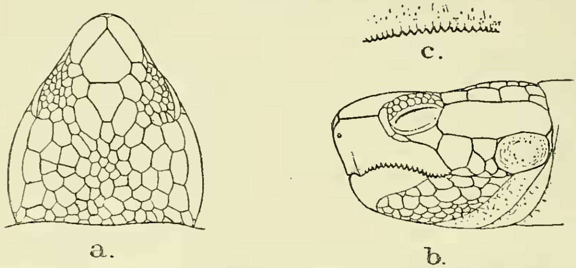
Sex.	Length in mm.	Breadth in mm.	Breadth per cent.	Depth in mm.	Depth per cent.	Abnormalities.	Collection.
Yg.	42	45	103·6	14	33·4	Small intergular.	British Museum, N.H.
„	60	60	100	19	31·7	Nine ribs reaching marginal region on each side, *i. e.* supernumerary 10th pair.	„ „
„	71	64	90	21	29·6	Twelve marginals on each side.	„ „
„	81	68	84	24	29·6	Supracaudal undivided.	„ „
Hgr.	85	77	90·5	...	...	....	Tring Museum.
„	89	76	85·5	26	29·3	Supracaudal undivided.	British Museum.
„	103	87	84·5	24	23·3	Posterior marginals strongly serrated.	Mus. Comp. Zool., Harvard.
„	105	82	78	30	28·5	Supracaudal undivided.	British Museum.
♀	119	96	80·7	27	22·7	....	Loveridge Collection.
♀	130	100	71·4	28	21·5	....	„ „
♀	133	105	79	30	22·5	....	„ „
♀	135	120	79	...	...	....	American Museum, N.H.
♂	135	102	75·6	30	22·5	....	Mus. Comp. Zool., Harvard.
♀	137	108	79	26	19	....	Loveridge Collection.
♂	139	100	72	29	20·8	....	Zool. Society's Gardens.
♀	140	110	78·5	...	...	(Skeleton figured).	British Museum.
♂	140	100	73	27	19·3	Four vertebrals; fourth costals uniting by median suture behind third vertebral. Correlated abnormalities in underlying bony plates.	„ „ (type).
♂	141	100	71	29	20·6	....	Loveridge Collection.
♀	142	107	75·4	36	25·4*	Supracaudal undivided.	Zool. Society's Gardens.
♀	146	107	73·3	33	22·6	Well-developed intergular (figured); twelve marginals on left side.	Loveridge Collection.
♀	146	113	77·4	32	22	....	British Museum (type).
♂	149	115	77·1	...	...	Intergular present, as large as a gular.	Tring Museum.
♂	150	108	72	30	20	....	Loveridge Collection.
♂	155	130	83·8	...	...	....	Smithsonian Institute.
♀	160	130	83·9	...	...	....	„ „

* This live specimen was greatly distended when measured.

nasals meeting each other by a mesial suture of variable length, usually between one-fourth and two-thirds length of præfrontal (*vide* text-fig. 2 a).

Horny coverings of sheaths of alveolar ridges of maxillæ and mandibles with regular, clearly-defined denticulations, 15 to 20 (usually about 20) on each outer, and 6 to 9 (usually about 7) on each inner maxilla; 12 to 15 on each outer and 5 to 9 or 10 on

Text-figure 2.



a. Upper surface of head. (Adult; nat. size.) b. Side view of head.
c. Horny teeth enlarged.

each inner mandible. Beak tricuspid, with one or two of these denticulations between each cusp. Sometimes the points of these odontoids look precisely like the regular teeth of an Agamoid lizard; but in other individuals they are not so well developed. They may be more so in the upper than the under jaw, or on the outer or the inner ridges, but whenever distinct are extremely regular (*vide* text-fig. 2 b, c). In all cases they are more developed in the horn than in the underlying bone.

Limbs.

Lower part of fore-limbs covered with large claw- or scale-like shields, three very much enlarged on the anterior surface above wrist; normally five well-developed claws.

Tibial portion of hind-limb often longer than radial portion of fore-limb, covered with irregular juxtaposed horny shields the size of those on the humeral portion of the fore-limb; scales on sole enlarged and claw-like in adults; normally four strong claws. In an abnormal specimen these claws are so overgrown that the outer one measures 13 mm. A group of enlarged tubercles on hinder side of thigh in some individuals.

The limbs are not nearly so club-shaped as in most species of *Testudo*; both wrists and ankles are supple and defined by a well-marked crease in the skin; the foot projects considerably (*vide* Pl. I.). This is especially marked in the young.

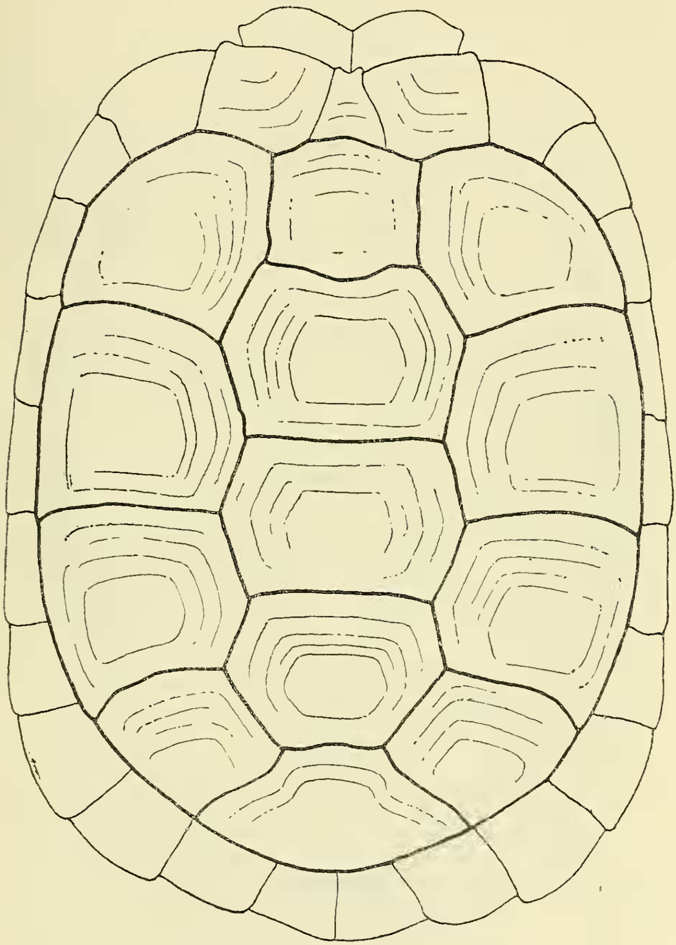
Tail.

Tail normal, much longer and stouter in the male than in the female.

Epidermal shields.

The epidermal shields are highly characteristic in form, but subject to great variation individually. In several specimens supernumerary shields and other abnormalities occur; for

Text-figure 3.

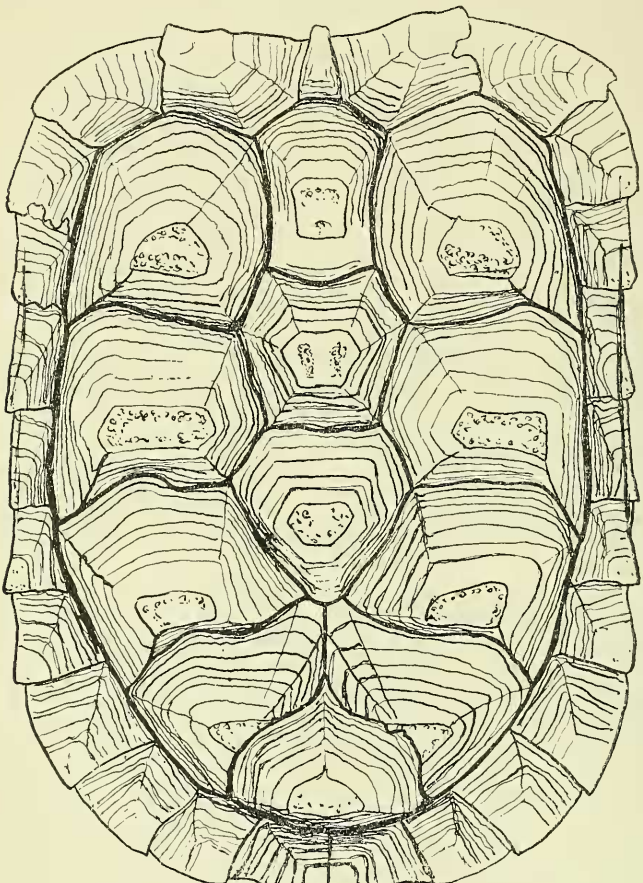


Epidermal shields of the carapace. (Adult; $\frac{3}{4}$ nat. size.)

instance, one adult has twelve marginals on the left side, one has twelve on both sides, and in one the posterior marginals form a deeply serrated border; the male type has only four vertebrals, one female has the third vertebral divided longitudinally, and two have extraordinary embossed vertebrals; three individuals possess an intergular. Mr. Loveridge mentions two specimens, which unfortunately escaped, in which small azygous shields occur, also several in which the supracaudal is single or semi-divided.

Each shield is also subject to considerable individual variation of size and shape.

Text-figure 4.



Sketch of carapace of male type-specimen, showing abnormalities in epidermal shields ($\frac{3}{4}$ nat. size).

The shield surfaces in the young are excessively rugose or coarsely granulated, each one bordered narrowly by a raised band of smooth horn; with age these rugosities wear smooth, but the ensuing growth-rings, also of smooth horn, are extremely regular, and the concentric striations between are deep and strongly marked. This applies to the plastron as well as the carapace.

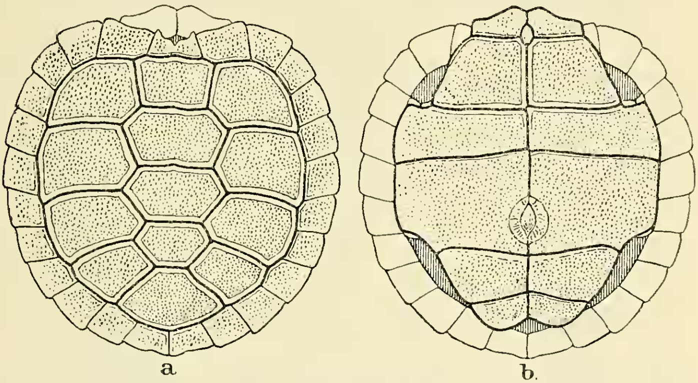
Nuchal shield very variable; much broader than long and cleft anteriorly in young specimens; about as long as broad to three times as long as broad, usually a little more than twice, and not, or but slightly, notched in adults.

First vertebral subtetragonal, usually slightly longer than broad, or as long as broad; the anterior border longer than the posterior, both convexly curved; lateral borders straight, slightly oblique. On the male type this shield is greatly elongated (*vide* text-fig. 4).

Second and third vertebrals hexagonal, broader than long, the suture between them usually a little shorter than the length of either shield, a little longer than the suture between first and second or third and fourth.

Fourth vertebral with very short posterior border, not more

Text-figure 5.



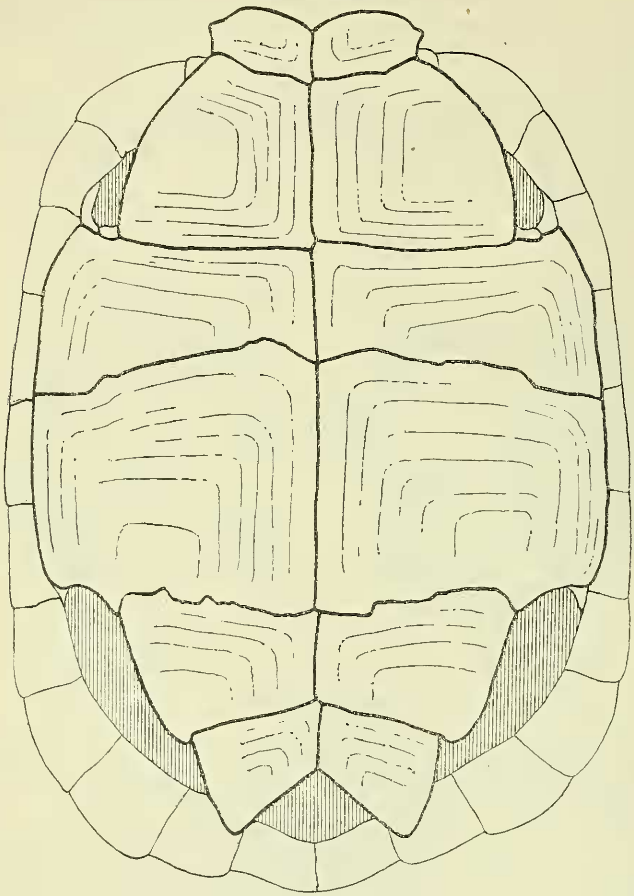
Young specimen, showing relatively broader shields (nat. size).
a. Carapace. b. Plastron.

than half length of suture between third and fourth. In the male type this shield is subtriangular or cordiform, and widely separated from the last vertebral by the fourth costals.

Fifth vertebral obtusely pointed and flat anteriorly, in the same plane with the preceding vertebrals; posteriorly its border is curved, and bent downwards sometimes very abruptly; the lower edge in some cases curves in so as to form an angle with the more obliquely set supracaudals.

Costals highly characteristic in form. In the ordinary *Testudo* the sutures between these shields form straight lines more or less at right angles to the long axis of the carapace; in *T. loveridgii* they form curves, particularly pronounced in the case of those between the fourth pair and fifth vertebral. The areolars are also excentrically placed. In *T. ibera*, for instance, the border around the areolar is about twice as broad in front as behind, and situated high up in the shield, the distance between it and the vertebrals being less than the distance between it and the costal posterior to it, and a quarter or less the distance between it and the marginals; in fact, the relative widths of the shield-borders

Text-figure 6.



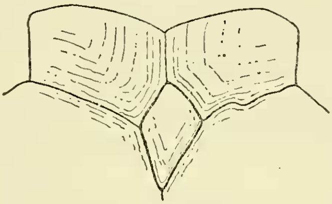
Epidermal shields of the plastron. (Adult; $\frac{3}{4}$ nat. size.)

(top : back : bottom : front) are roughly expressed by the geometrical progression—2 : 4 : 8 : 16. In *T. loveridgii* this ratio is better expressed—4 : 2 : 4 : 5 or 4 : 1 : 4 : 6, the areolar being midway between vertebrals and marginals, but situated very far back in the shield. The areolar of the fourth costal is often actually in contact with the anterior margin of the fifth vertebral. This condition is not marked in the young, but is accentuated by each growth-ring. The fourth pair, in the male type, as already remarked, are broadly in contact mesially, in front of the last vertebral; in no other instance does this occur although they are sometimes in close proximity. The abnormal form of these shields on the male type is shown in text-fig. 4.

The second costal is usually about equal in width to the third vertebral.

The marginals are also extremely characteristic and very greatly reduced in depth. The first pair are normal in outline but a little longer than deep; the second and third are about one and a half times as long as deep; fourth to eighth greatly reduced, once and a half to twice as long as deep, as against about two-thirds long as deep in *T. ibera*; ninth and (or) tenth deepest, a little deeper than long; tenth and eleventh similar but slightly smaller. In the young the marginals are more or less uniform, as deep as broad or a little deeper; the sutures dividing them are somewhat oblique, making them rhombic in shape (*vide* text-fig. 5 **a**).

Text-figure 7.



Intergular shield (nat. size).

The supracaudal is paired in all the specimens examined with the exception of a female living in the Zoological Society's Gardens, and three young specimens, in which it is single.

The epidermal shields of the plastron are not peculiar in any way (*vide* text-fig. 6).

Gulars moderate, truncate and rounded anteriorly, forming together a bow-shaped edge, projecting beyond the carapace and forming a support for the animal's chin; lateral edges shorter than the median suture; gulo-humeral sutures directed obliquely backwards and inwards, meeting each other at an angle of 60° to 140°.

An intergular is present in three out of twenty-three specimens. In the smallest specimen it is small but distinct (*vide* text-fig. 5 b); in one female it is somewhat smaller than a gular (*vide* text-fig. 7), and in a male it is well developed and as large as a gular. In all three it is protuberant and kite-shaped, the short sides in front.

Humerals about twice as broad at humero-pectoral suture as from apex to apex, or their median suture.

Pectorals narrow, median suture two-fifths to three-fifths length of median humeral suture.

Abdominals more or less square, median suture two to four times length of median pectoral suture.

Femorals very variable, median suture usually longer than median pectoral suture ; postero-lateral corners projecting beyond lateral edges of anals.

Anals.—Ano-femoral sutures slightly oblique, directed forwards ; lateral borders at right angles to them ; median sutures short, each anal cut away posteriorly and ending in a pronounced point of variable shape, the resulting cleft between them forming an angle of 90° to 120°. The width and depth of this cleft is apparently not dependent on sex, as one would suppose from the great difference in the relative sizes of their tails.

The inferior surfaces of the marginals which cover the bridges are extremely narrow, from three to four times as long as deep.

SKELETON.

Besides the complete skeleton of one adult, and the radiographs of the types, a considerable amount of accessory material has been available. An excessively interesting individual, in which development had been arrested at a still earlier stage, decomposed in transit, thus enabling me to use most of the skeletal parts for study. In this specimen the bony plates were as thin as tissue-paper and extraordinarily flexible. Parts of other tortoises also disintegrated and formed interesting checks on the first skeleton.

Of the young, an X-ray plate shows that the limb-girdles are normal, as in the adult. The structure of the carapace has been studied in a series of six, ranging from 42 to 82 mm. in length ; in these it was dissected off and the inside aspect cleaned. A complete preparation of both carapace and plastron was made from a specimen 60 mm. in length, and the plastron of the 42 mm. individual studied, without its removal, from the inside.

This material was amply sufficient to show the normal structure and development, besides some interesting variations of the skeleton of *T. loveridgii*, and to form highly interesting comparisons with other species.

The word "plate" is repeated after the name of each dermal bone, in order to distinguish them from the epidermal shields of the same names.

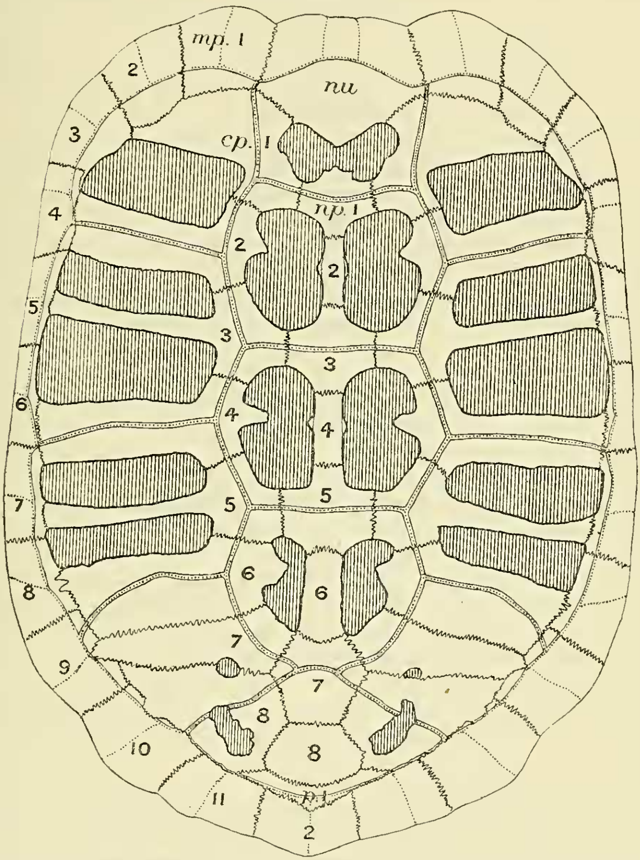
The bony carapace of the adult.

In general appearance the bony carapace is extraordinary. Such portions of the neural and costal plates as are present, are formed of translucent bone, and when damp are springy and flexible, making it possible to depress or elevate the carapace as if it were supported upon springs.

Where the epidermal shields form sutures with each other, the bone beneath is deeply grooved, sometimes forming perforations, but always markedly transparent (*vide* Pls. II. & III. and text-fig. 8).

Beneath the vertebral shields are four large fenestræ shaped like butterflies: the first is entire; second, third, and fourth

Text-figure 8.



Bony carapace of an adult, viewed from above ($\frac{4}{5}$ nat. size). Fenestræ |||||; deep grooves beneath shield-sutures ═══; neural plates *np.*; costal plates, *cp.*; marginal plates, *mp.*; nuchal, *nu.*; pygals, *p.*

divided mesially each by a bony bridge formed of rudimentary neural plates; the first and fourth are small compared with the second and third (*vide* text-fig. 8).

Beneath the costal shields there are also large fenestræ similar in shape to the shields under which they are situated. That under the first is entire; those beneath the second and third divided mesially by a narrow transverse bridge of bone formed by the third and fifth costal plates. There is no large fenestra beneath the fourth in the normal adult.

Nuchal plate moderate, posterior corner free, forming anterior edge of first median fenestra, which exposes the ninth vertebra.

First neural plate (text-fig. 8, *np.* 1) very much reduced in comparison with that of a normal *Testudo*; anterior edge pointed, bordering first fenestra by which it is separated from the nuchal plate; narrow lateral limbs, uniting by short sutures with first pair of costal plates (*cp.* 1); narrow posterior limb, entering into second median fenestra, where it forms part of the dividing bridge and unites by short suture with the second neural.

Second neural plate (*np.* 2) vestigial, barely wider than the vertebræ beneath, with straight lateral edges, uniting by short sutures with preceding and succeeding neurals, and forming the main part of the fenestral bridge.

Third neural plate (*np.* 3) octagonal, very much reduced, oblique edges free, curved invertedly, bordering the inner corners of the second and third fenestræ, which this plate divides one from the other by uniting with the second costal plates (*cp.* 2) by narrow sutures, thus forming a narrow bridge between them; also forming similar connections with second and fourth neurals.

Fourth neural plate (*np.* 4) similar to second but somewhat broader in proportion, forming the longitudinal dividing bridge across the third median fenestra.

Fifth neural plate (*np.* 5) precisely similar to the third.

Sixth neural plate (*np.* 6) similar to second and fourth but broader still, dividing fourth median fenestra, which is, however, much smaller than the two preceding.

Seventh neural plate (*np.* 7) normal, hexagonal, without free edges, uniting by six sutures with the sixth and eighth neural, and seventh and eighth costal plates respectively; those formed with the eighth costals slightly longer than the others.

Eighth neural plate (*np.* 8) normal, sub-tetragonal, without free edges, uniting by oblique sutures with the eighth costal, and by transverse ones with the seventh neural and first pygal plates, the latter suture the longer and curved.

First pygal plate broadly cordiform or septagonal, set almost at right angles to the horizontal plane of the neurals, curving in where the marginal epidermal shields meet the fifth vertebral, and curving out more obliquely to form a point beneath the supracaudal shields. It forms sutures with the eighth neural and costal, eleventh marginal (*mp.* 11), and second pygal (*p.* 2) plates, that with the eighth neural about twice as long as any of the others and curved invertedly.

Second pygal normal, equal in size to the eleventh marginal plate.

First costal plates (*cp.* 1) shaped like wings, uniting by short sutures with the lateral edges of first neural (which forms a bridge between them) and second costal plates, thus separating the first lateral fenestra from the first and second median fenestræ on each side; the broadly curved anterior edges form an uninterrupted suture with part of nuchal, whole of first and second, and inner corner of third marginal plates in most cases, but sometimes the distal portion is undeveloped, and therefore less wing-like, or cleft, or perforated beneath the shield-sutures (*vide* text-fig. 9).

Text-figure 9.

Left first costal plate from beneath, showing perforation beneath vertebro-costal shield-suture; distal end incompletely developed, and cleft. (Nat. size.)

Fenestræ between first and second costal plates are from front to back as long as one marginal, from side to side two or three times this length.

Second costal plates (*cp.* 2) slender, feebly developed, widely separated from the neural; anterior and posterior heads forming narrow sutures with first and third costal plates beneath costo-vertebral shield-sutures, main arms supporting transverse costal shield-suture, and uniting distally with the fourth marginal plate. Length of each (measured from end to end) three times breadth (measured from front to back); median head forming a short-pointed process directed inwards, but widely separated from the vestigial second neural plate. The X-ray plates of the types show that these processes are sometimes connected with the vestigial rib-heads by the ligament-like periosteal tissue of the absorbed rib.

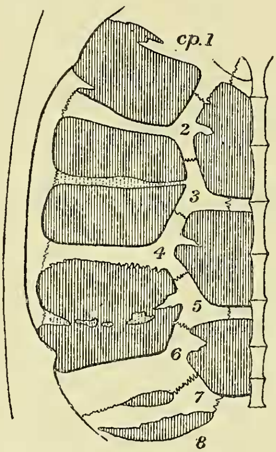
Third costal plates (*cp.* 3) extremely slender, rib-like, and feebly developed. Main arms half or less than half breadth of those of second, from which they are separated by a fenestra about half as broad as those preceding. Each has three heads, each one of which is twice as broad as the main arm, the median uniting by suture with the third neural plate, thus forming a bridge between second and third median fenestræ on each side; anterior and posterior heads directed obliquely outwards, similarly united with the corresponding heads of second and third costal plates, which are directed obliquely inwards beneath the costo-vertebral shield-sutures.

In the specimen in which development has been arrested at a very early stage, only the merest traces of bone-deposit are present in place of the rib-like arms of these plates (*vide* text-fig. 10).

Fourth costal plates (*cp*. 4) in form precisely like second, twice or more than twice width of third, sometimes with very ragged edges; widely separated from neural by third median fenestræ, forming a suture with sixth marginal plates, sometimes with corner of seventh also. Fenestra between third and fourth similar in size and shape to that between first and second, about twice width of that between second and third.

Fifth costal plates (*cp*. 5) precisely like third in every way, connecting by suture with seventh marginal plates. Fenestra

Text-figure 10.



Carapace of adult arrested at an earlier stage in development. (Left side, from within ; $\frac{1}{2}$ nat. size.)

between fourth and fifth similar to that between second and third, about half width of that between third and fourth. In the poorly developed specimen already referred to (text-fig. 10) the rib-like limb is represented by a few bone-granules in isolated patches.

Sixth costal plates (*cp*. 6) similar to second and fourth, but rather more developed. Anteriorly narrowly in contact with fifth beneath the vertebro-costal shield-sutures, otherwise separated by fenestræ slightly narrower than any of the preceding. Central head in closer proximity to the neurals than those of second and fourth; the dividing fenestra about half as large as in the former instances. Posterior edge quite straight, forming a suture with seventh costal plate throughout its length from fenestra to ninth marginal, excepting in the abnormal specimen, in which it is partially separated from the seventh by an elongated fenestra.

Seventh costal plates (*cp.* 7) straight, with angular head and pointed distal end which is projected some distance into middle of ninth marginal. Anterior facet of head free, bordering fourth vertebral fenestra, posterior forming suture with seventh neural plate; main anterior border forming suture with sixth costal from end to end, posterior border forming a similar suture with eighth. On the upper third of the suture between the seventh and eighth costal plates there is a small oval fenestra,

Text-figure 11.

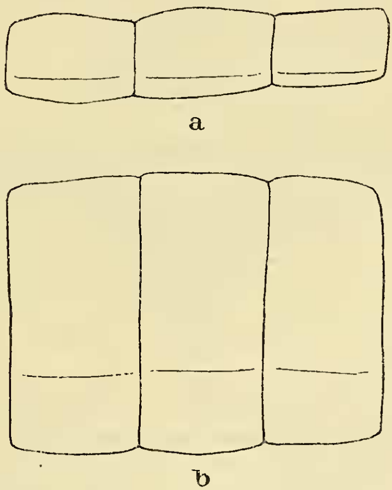


Diagram of marginals 5, 6, and 7. a. *T. loveridgii.* b. *T. ibera.*

smaller on one side than on the other in the individual figured, but of variable size in others. It is always very ragged in outline.

Eighth costal plates (*cp.* 8) pentagonal, broad, with the exception of the very small fenestra described above, completely in contact with the surrounding plates—*i.e.*, seventh costal, seventh and eighth neural, first pygal, ninth, tenth, and eleventh marginal plates. A small triangular process is projected into the anterior portion of tenth marginal. A small kidney-shaped fenestra with jagged edges pierced above the ilio-sacral region, anteriorly reaches just beyond the groove made by the fourth costal and fifth vertebral shields and proceeding backwards almost to the eighth neural.

Presumably this fenestra and the small oval one between the seventh and eighth costals are all that remain of the large kidney-shaped one, similar to those between the preceding costal and neurals, which is present in youth.

The marginal bones are somewhat wider than the corresponding shields; first, second, and third markedly so; sixth to tenth deeply notched in the middle for the reception of spurs from the corresponding costal plates. Fifth, sixth, and seventh enter into the composition of the plastron beneath, and will be dealt with as part of the plastron.

When one considers the great depth of the lateral marginals in ordinary tortoises in comparison with their abnormal shallowness in *T. loveridgii*, the shallow carapace of the latter is to some extent explained. In text-fig. 11 the fifth, six, and seventh marginal plates, drawn diagrammatically, of *T. loveridgii* and *T. ibera* are compared.

The bony plastron of the adult.

The bony plastron is also composed of bone thin to translucency. In the centre there is an enormous diamond-shaped fenestra reaching from ento- to xiphiplastron, and side to side from marginals to marginals. It is very ragged in outline, variable in size, and lies beneath the pectoral and abdominal shields, so that the greater part of the abdomen is unprotected by bone (*vide* text-fig. 12).

Epiplastrons (*ep.*) shapely, oblique, moderate in size; posterior borders serpentine.

Entoplastron (*ent.*) in the shape of a diamond, the anterior and posterior corners of which have been truncated; posterior margin free, corresponding with the humero-pectoral shield-suture above, entering into the central fenestra, into which a sharp bony spur projects, representing the tip of the sternum, which is fused to the inner surface of this plate in the normal way.

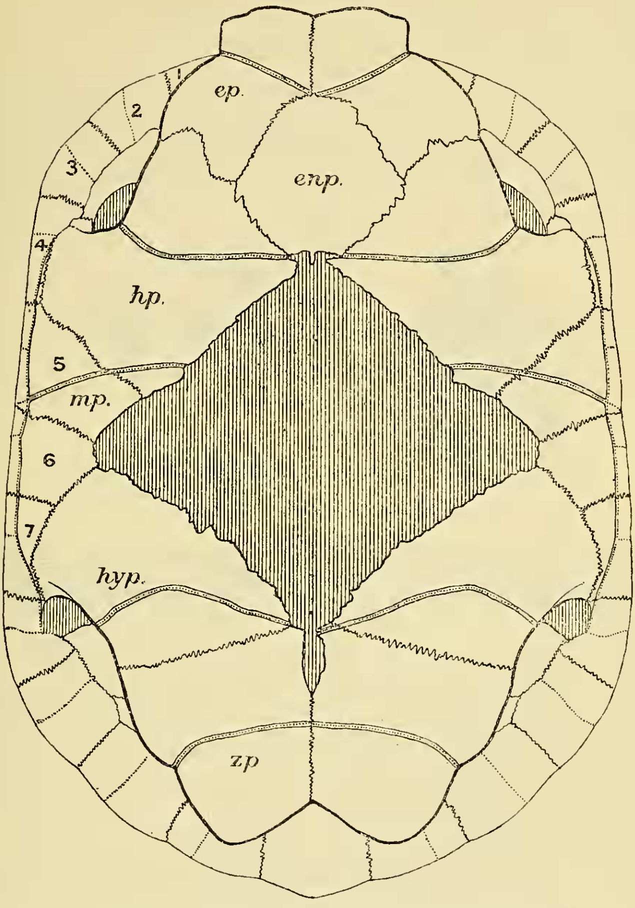
Hyoplastrons (*hp.*) very small, rectangular, obliquely set; separated from each other by the anterior angle of central fenestra; widely separated from the hypoplastrons by marginal plates.

Marginal plates (*mp.*) 5, 6, and 7 enter into the composition of the plastron on each side of the fenestra, spreading obliquely inwards to a most unusual degree, number 5 running beneath the pectoral shields to the abdominal, and terminating with a free oblique edge in the central fenestra; number 6 borders the lateral corner of the central fenestra on each side.

Hypoplastrons (*hyp.*) completely separated from each other by the posterior angle of the central fenestra; produced to form part of the posterior plastral lobe.

Xiphiplastrons (*zp.*) form slightly oblique sutures with the hypoplastrons; their anterior median corners enter into the

Text-figure 12.



Bony plastron of an adult, viewed from without ($\frac{4}{5}$ nat size).
Fenestra ||| ; deep grooves beneath epidermal shield-suture ═══ *; epiplastrons, *ep.*; entoplastron, *enp.*; hyoplastrons, *hp.*; hypoplastrons, *hyp.*; xiphiplastrons, *zp.*; marginal plates, *mp.*

posterior corner of the central fenestra, which separates them from each other anteriorly; a broad open cleft posteriorly; lateral edges bi-lobate.

* The groove beneath the median longitudinal shield-sutures is equally deep, but is not marked, as it would obscure the bony ones beneath.

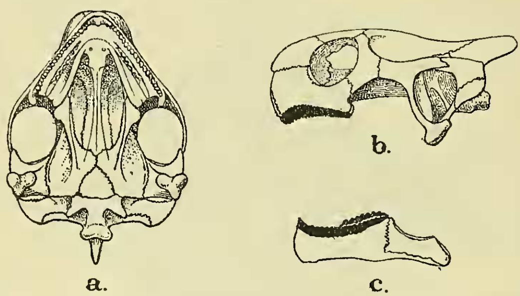
Skull.

Differing from the common *T. ibera* in the following particulars:—

The præfrontals are larger than the frontals, and widely separated from the post-frontal bridge; temporal and post-orbital arches stouter in proportion, especially the latter; *annulus tympanicus* larger, stapes as slender as a hair.

Maxillary with three alveolar ridges, the inner one of which is comparatively weak, the outer one, or maxillary edge, denticulated with what appear to be minute pointed teeth of the acrodont type, but which have not the composition of true teeth; the number is about 20 on each outer, and about 7 on each inner, maxillary

Text-figure 13.



Skull of adult (nat. size). a. Palatal view (horny sheaths not blackened). b. Side view (horny sheaths blackened). Horny sheath of maxillary partially dissected away to show denticulations in the bone itself. c. Mandible (horny sheaths blackened).

ridge. One or two similar denticles between the cusps of the præmaxillary. These denticles are so fragile that if the adherent horny sheath is removed in the usual way, they are completely destroyed, but they can be clearly seen without a lens if the horn is partially removed. In text-fig. 13 this has been done, and the remaining horn blackened in the profile view, in order to distinguish it from the maxilla.

All the cranial foramina seem to be proportionately small.

The mandible has both its alveolar ridges denticulated in the same manner as the maxilla. In the figure the horny sheaths, in this case entire, are blackened.

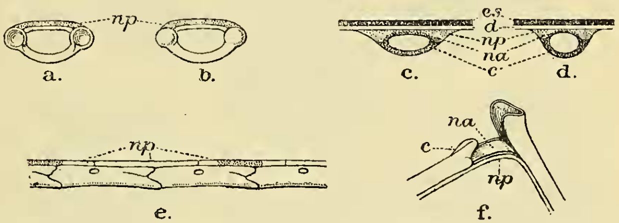
Vertebral column.

First eight (cervical) vertebræ as in *T. ibera*.

The dorsal vertebræ (ninth to eighteenth in the complete series) differ profoundly from the ordinary pattern; they are entirely without spinous processes and the centra are greatly depressed instead of compressed, and hollowed to a thin shell for the reception of the spinal cord, the vertebræ being thus a simple depressed tube, adherent to the bony neural plates of the carapace. In all other species the vertebral column is separated from the carapace by wide arches, the contact with it being formed by long thin neural processes; in no case is the main column, even narrowly, in contact (excepting *T. tornieri*).

It is in some cases impossible to detect what remains of the neural arch in a section, for it has degenerated to such an extent that in some individuals it appears to be wanting altogether. Possibly it is absorbed to a variable extent in the same manner as the ribs. In the vertebral sections figured (*vide* text-fig. 14), it seems to be represented by an extremely thin layer beneath the neural plate, forming a meagre roof to the neural canal. The specimen to which it belongs, however, is the most degenerate of any that have been examined. More normal individuals, however, cannot be spared for the necessary dissection. Figs. **c** and **d** show diagrams of sections through the middle and towards the anterior end of the eleventh vertebra;

Text-figure 14.



Diagrams of mid-dorsal vertebræ. **a.** Anterior end. **b.** Posterior end. **c.** Section towards one end. **d.** Section through middle. **e.** Side view of vertebræ with lateral expansions of neural plates cut off. **f.** Two vertebræ bent apart, to show thinness and flexibility of the combined neural plate and neural arch. Epidermal shield, *es*; dermis, *d*; neural plate, *np*; neural arch, *na*; centrum, *c*.

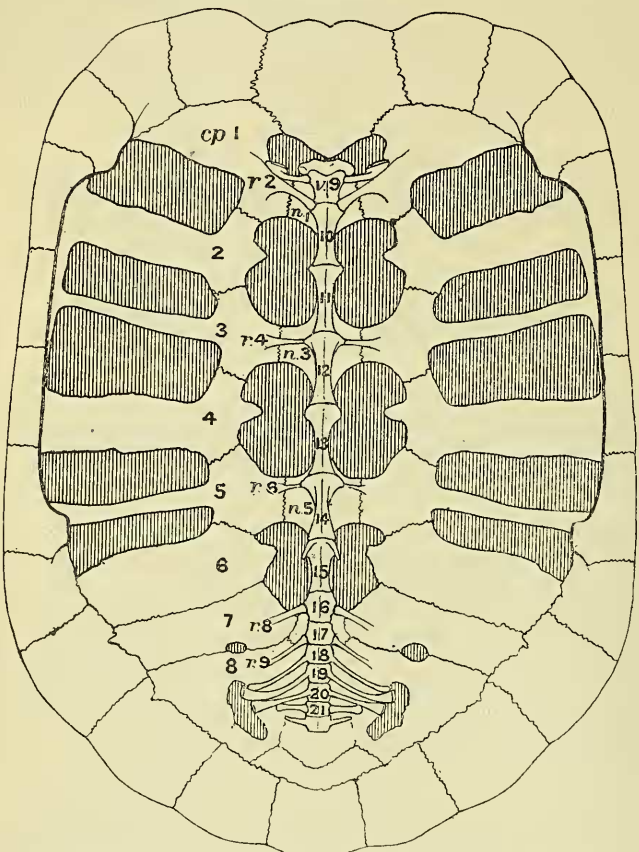
figs. **a** and **b**, the vertebra viewed from each end; fig. **e**, the twelfth and thirteenth with part of eleventh, side view, with the lateral portion of the third neural plate cut through; fig. **f**, the twelfth and thirteenth, bent apart to show the thin flexible covering of the neural canal. The relative positions of the articulation of the vertebræ and the neural plate sutures vary, usually alternating with each other. The points of juncture between the 5th and 6th neural plates and 14th and 15th vertebræ, however, coincide, one above the other.

The ninth vertebra is, of course, highly specialised for the articulation of the neck. The facets for the articulation of the first (non-functional) ribs are situated at the extreme anterior end. Vertebræ ten (2nd dorsal) to thirteen are progressively more elongate, and have the tubercles for the articulation of the rib-heads at the extreme anterior end on each side as in the ninth; in some of the young, articulation takes place at the juncture of each consecutive pair of vertebræ. Fourteenth to seventeenth become progressively shorter, and the facets for the corresponding rib move further backwards in a lateral ridge as the ribs become directed obliquely in this direction. Eighteenth nineteenth, twentieth, and twenty-first vertebræ progressively shorter, their diapophyses elongate, slender, distally in contact and supporting the iliac crests, those of the nineteenth the longest. Diapophyses of anterior caudal vertebræ also elongate. Caudals normal, twenty-four in number, stouter in the male than in the female, according to the radiographs.

Ribs.

The ribs may be considered as absent in the adult, the part

Text-figure 15.



Bony carapace of an adult, from within ($\frac{1}{5}$ nat. size), showing vertebræ, and vestigial ribs. (Ribs not entirely absorbed in this specimen.) *

normally adherent to the carapace having become completely absorbed. The free or capitular portion is sometimes present as

* Sutures between costal plates 2, 3 and marginal plates 4, 5, accidentally omitted.

a vestigial thorn-like structure, but is more often absent altogether, or represented by a thin ligamentous simulacrum (*vide* Pls. II. & III.).

The first pair, which in all tortoises are rudimentary, are normal. The second (first functional) have the free capitular portion sometimes present, although reduced, adherent terminally to the first costal plate, and in contact with the first pair in the usual manner (*vide* text-fig. 15). Third pair absent or vestigial.

Fourth pair, when present, similar to the second, but usually as slender as a hair; in contact with third pair of costal plates. Fifth pair absent or vestigial. Sixth pair like the fourth, but still more vestigial and directed slightly backwards. Seventh pair absent or in some specimens present, and bridging the fenestræ and meeting the corresponding process of the sixth costal plates, directed slightly backwards. Eighth pair rather depressed, directed still more backwards, in contact with the seventh pair of costal plates just in front of the seventh neural plate. Ninth pair slender, directed strongly backwards and flattening out beneath the head of the eighth costal plates.

In the young specimen (60 mm. long) described in the next chapter, a tenth pair of ribs are present.

Pectoral girdle.

The bones of the pectoral girdle and fore-limbs, as compared with those of *T. ibera*, are slender, and the coracoids are not so strongly dilated; in other respects they are similar (*vide* Pls. II. & III.).

Pelvic girdle.

The bones of the pelvic girdle and hind-limbs, also compared with those of *T. ibera*, are somewhat more slender and those of the pelvis less dilated (*vide* Pls. II. & III.). The ilia are not fixed above as in the ordinary tortoises, as they terminate just beneath the last median fenestræ in the carapace, whilst in tortoises with a solid carapace they articulate with a bony prominence beneath the eighth costal plate.

Development.

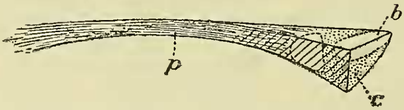
Until April of this year, only adult or extremely young specimens were available, and it was, therefore, only possible to guess at the intermediate skeletal forms. Mr. Loveridge has, however, now sent over a series of young and half-grown, which illustrate the processes which are taking place and corroborate my earlier speculations.

Ribs.

In the young the ribs are perfectly normal (*vide* text-figs. 17, 18) but step by step they disappear. The portion adherent to the carapace becomes flattened, and disappears in a manner similar to that met with in other members of the genus. The first portion to become completely absorbed is that which underlies the oblique connecting bridges between the costal plates, which in turn underlie the vertebro-costal epidermal shield-sutures: that is to say, the point where the rib becomes adherent.

The capitular free portion of the rib absorbs in a peculiar way. At 71 mm. these free ribs still appear to be present when the carapace of a spirit specimen is raised; when explored, however, they prove to be chiefly composed of soft pliant material, like ligament. At 81 mm. there is still a splinter-like rib within this soft material, but this becomes more and more wasted by absorption, until it is lost absolutely in the adult, or represented by a tiny thorn-like splinter one or two mm. in length—the extreme capitulum of the original rib. Mr. Burne has very kindly investigated the structure of this soft portion, excised from a young specimen. Longitudinal sections show that with

Text-figure 16.



Microscopic section through capitulum of absorbing rib (× 100), in which almost nothing but periosteum is left. (After a sketch by Mr. Burne.) Periosteal fibres, *p*; cartilage, *c*; areas of calcification, *b*.

the exception of two small areas of calcification in the capitulum itself, no bone is left (*vide* text-fig. 16). These areas are situated in a part of the original cartilage; the rest of the section shows nothing but parallel bundles of what appears to be connective tissue. Near the edge of the sections there are, however, a row of multi-nucleated cells which Mr. Burne considers to be osteoclasts. He says: "I presume what happens is that the bone after being formed in the rib is absorbed by these osteoclasts, and the periosteum—possibly thickened—is left, forming a simulacrum of the rib." There is no doubt in my mind that this is the right interpretation; also that this process of absorption, carried only to an early stage, is responsible for the excessive slenderness of this portion of the ribs in other species.

The carapace.

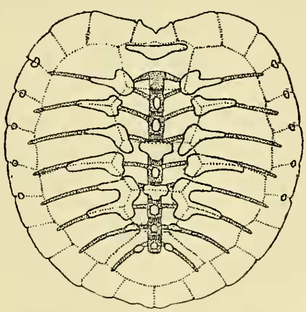
In a specimen 42 mm. in length, probably newly hatched or only a few months old, the plates are commencing their development, and are at a particularly interesting stage (*vide* text-fig. 17).

The nuchal is more or less fully formed within the marginal ring, but does not extend beyond. The neurals, excepting the third and fifth, consist of minute oval areas of yellowish bone-granules towards the anterior of each underlying vertebra. The third and fifth are laterally dilated to some extent, the fifth being almost in contact with the head of the fifth costal plate. These two neurals underlie the two middle vertebral shield-sutures. The thin layer of coarse bone-granules which composes each one of them is distinguishable without a lens. In pulling up the carapace, quite half of these plates separated easily from the vertebræ and adhered to the carapace, or rather to the dermis, which shows that they are not completely fused with the vertebræ at this stage.

The costals are slightly more developed, and are disposed as follows:—The vertebral and costal epidermal shields meet each other in a zigzag suture which has seven angles. At each of these, three shields meet corner to corner. It is beneath these points that the centres of the incipient costal plates are located. They are therefore alternately nearer to, and further from, the vertebræ. Those nearer to them tend to develop proximally, and are more or less rhomboidal in shape, and those further away develop distally down the rib, and are more triangular, the apex pointing towards the marginal region.

The first, second, and third are not quite in contact with each other, the third, fourth, and fifth are nearly in corner to corner

Text-figure 17.



Carapace of newly-hatched young, from without (nat. size).
Epidermal shield-sutures ·····················; vertebræ and ribs :·:·:·:·:.

contact, the fifth and sixth are joined by oblique suture as in the adult, forming an oblique bony bridge beneath the shield-suture. The seventh and eighth are but commencing their formation.

The pygals are absent altogether.

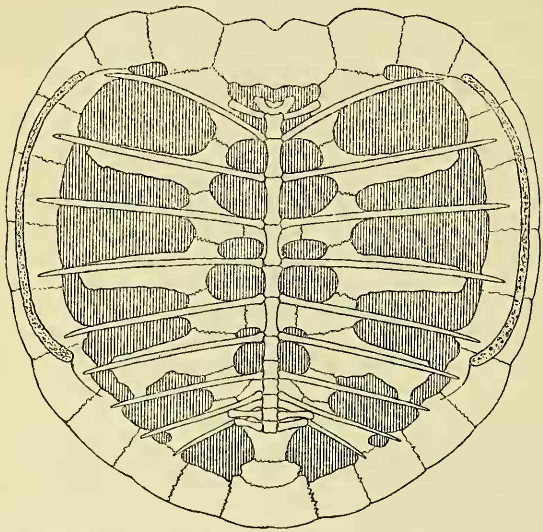
The marginal plates are not recognizable as such at this stage, but minute groups of bone-granules are detectable beneath the shield-sutures between marginals three to eight. Posteriorly they are not visible, although their primary particles may be present in the dermis.

At about 60 mm. the eight pairs of ribs (2nd to 9th) are still distinct and of normal length, but are modified, the proximal 5 mm. having become very slender, and the remainder flattened and adherent to the dermal costal plates where these are present. In the particular specimen figured a ninth pair of ribs are fully developed, and reach the marginals on both sides.

At this stage (*vide* text-fig. 18) the development of the dermal bones of the carapace is well advanced, showing most clearly how the carapace of the adult is formed. The anterior and median portion is developed almost as much as in the adult, but posteriorly large fenestræ occur beneath the fourth costal and fifth vertebral shields, which (fenestræ) are almost entirely roofed in with bone in the adults.

The nuchal and marginal plates are fully formed. The neurals are of the adult pattern, but they are narrow, thin, and feebly developed anteriorly, becoming progressively broader posteriorly, the seventh and eighth are the broadest, followed by a much narrower first pygal. The first pygal is not well developed, and is separated from the last costal plate on each side by a very wide,

Text-figure 18.



Carapace of young specimen 60 mm. in length, from within ($\frac{7}{8}$ nat. size).

subtriangular fenestra, which is represented in the adult by a small one of ragged outline in the last costal plate itself.

From the study of this one stage it is easy to reconstruct the development of the bony carapace of the adult, and, by logical conclusion, to suggest a manner in which a solid carapace can be formed.

Costal plates one to six are similar in form and arrangement to those of the adult, excepting that they do not reach the marginal rib by about 3 mm. In the case of the first, the shortness of the plate causes a small fenestra to be discovered between the underlying rib and the anterior marginal plates.

At this stage one sees the relative positions of true ribs and costal plates, which are not clear in the ribless adults. The main limbs of the second, fourth, sixth, and eighth costal plates are very broad, narrowly bordering the underlying rib anteriorly but projecting widely beyond its posterior edge. The alternating third, fifth, and seventh are but feebly developed, and are very little broader than the underlying rib, which they cover, and border narrowly and equally. This alternating arrangement of the breadth development, which takes place posterior to the companion rib, accounts for the relative widths of the lateral fenestræ in the adult, in which the slender costal plates are preceded by a narrow fenestra, and succeeded by one at least twice as broad, the general effect being a single fenestra the shape of the epidermal shield, bridged by a slender rib-like costal. The same principle applies to the formation of the plates beneath the vertebral shields. In this case the first, third, fifth, and seventh neurals are well developed (progressively as already noted), and form lateral sutures with the corresponding well-developed heads of the corresponding costal plates. The broad bridge of dermal bone thus formed is over and posterior to the free underlying rib-head. This makes the segment of the median fenestra immediately following, half the width of the remaining segment on each side of the vertebræ, a similar arrangement to that met with in the case of the lateral fenestræ. The alternating second, fourth, and sixth neural plates are feebly developed, barely wider than the underlying adherent vertebræ, and are widely separated from their corresponding costals, which, though they are broadly developed distally, are not continued proximally. The large kidney-shaped fenestra in the dermal bone is, however, bridged by the true rib beneath; a slight deposit of dermal bone on the distal end of this rib-bridge forms the feeble, pointed apical head of the costal plate which projects into the fenestræ at a later stage when the rib itself has absorbed.

Thus the broad neuro-costal bridges are continuous with the slender main-limbed costals, and the undeveloped neurals are connected by the free portion of the rib with broad costal main limbs. The bony bridges formed by the oblique heads of the costal plates, and which separate the median from the lateral fenestræ (beneath the vertebro-costal epidermal shield-sutures), are about as wide as their neighbouring broad costal or neural plates. In the same way narrow anterior sections of the median fenestræ are opposite the wide and posterior sections of the lateral fenestræ, and *vice versa*.

In the young of this size there is one great difference in the stage of dermal bone development, namely that of the seventh and eighth costal plates. In the adult, the seventh, although narrow, normally forms an uninterrupted suture with the sixth and eighth from the last median fenestra to the marginal region. At the present stage, the seventh is similar to the slender third and fifth costals, and the eighth is similar to the broad second, fourth, and sixth costals, the seventh being separated from the eighth by a wide fenestra, represented in the adult by a small fontanelle, and from the sixth by a narrow one, absent in the adult; the latter fenestra, however, is divided into two by the contact of the posterior corner of the end of the dilated sixth with the seventh costal, about 3 mm. from the marginal plates. This is caused by the relative positions of the implicated ribs, which become closer together posteriorly as the vertebræ become progressively shorter. For this reason, the eighth costal plate in this specimen completely roofs over the ninth and tenth (abnormal) ribs, the intervening space between them being no broader than the entire second costal plate (compare text-figs. 18 and 15).

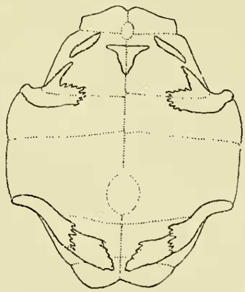
Therefore, in the first instance (42 mm.) it is the central portion of the carapace which is the most developed; later (60 mm.) the plates are more or less equally developed all over, with the exception of the neurals, which are progressively enlarged posteriorly. Continuing up the series (71, 81, and 89 mm.), the first, second, fourth, sixth, and eighth costal plates expand in length until they form sutures with the marginals; the third and fifth become the slender rib-like plates of the adult form; and the posterior portion of the carapace from the seventh costal to the pygal plates becomes roofed in with bone by the expansion of the seventh and eighth costal plates.

The anterior part of the carapace in the adult, therefore, is arrested at an earlier stage in its development than the posterior.

The plastron.

At 42 mm. the plastron is in the initial stage of development (*vide* text-fig. 19); all nine bones are present, but very small, thin, and for the most part widely separated from each other. The epiplastrons are merely small strips of bony deposit beneath

Text-figure 19.

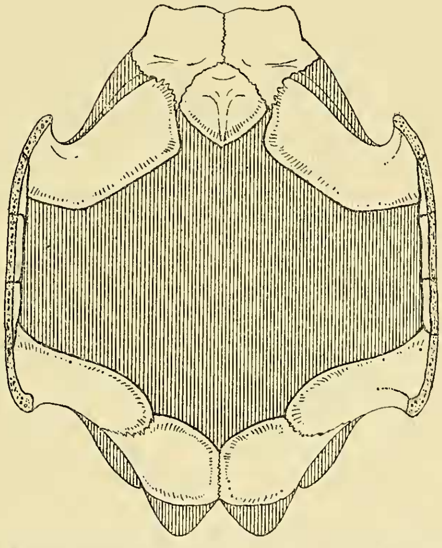


Plastron of newly-hatched young, from without (nat. size).

the anterior portion of the pectorals. The entoplastron is better developed, and subtriangular in shape. The hyoplastrons are ragged in outline, and not in contact with epiplastrons or entoplastron. Hypo- and xiphiplastrons narrow and in sutural contact, forming a narrow, bony band running obliquely across the hind lobe. The xiphiplastrons, however, do not meet each other.

In the 60 mm. specimen (*vide* text-fig. 20) the median fenestra is much broader in proportion than in the adult, reaching almost from edge to edge of the plastron. Marginal plates five, six, and seven, which in the adult are produced inwards for a considerable distance, only overlap the line of their corresponding epidermal shields to a small extent, and are about equal, not graduated in depth as in the adult (*vide* text-figs. 12 & 20). The epiplastrons are more or less pentagonal and not well developed posteriorly at their outer corners, but are in contact with the

Text-figure 20.



Plastron of young specimen, 60 mm. in length, from within (nat. size).

hyoplastrons and the entoplastron. Hyoplastrons narrow and not in contact with the entoplastron, or with the fifth marginal plates, with which in adults they form long oblique sutures. Hypoplastrons slender, widely separated from each other, and only narrowly in contact with the sixth marginal plate; they form short sutures with the equally slender xiphiplastrons.

Further development takes place principally on the inner borders of the plastral plates until the central fenestra has assumed the regular diamond-shaped form of the adult in this species (compare text-figs. 19, 20, and 12).

Discussion.

The morphogeny of the carapace and plastron.

The primitive plastron, therefore, and the delicate network of dermal bone which forms the carapace of the adult *Testudo loveridgii*, are brought about by arrested development. The fenestræ have not been formed in the completed structures by absorption, and do not increase in this manner with age as supposed. The relative thickness or breadth of the plates depends on individual variation, specimens of abnormal fragility having had their development in this respect cut short at an earlier stage than the average individual. This principle also applies to such species as *Testudo polyphemus*, in which the carapace is said to become thin and form fenestræ with age. A specimen in the British Museum Collection of 210 mm. (76. 1. 36. 6) and a half-grown specimen of 135 mm. (73. 8. 13. 25) have both carapaces and plastrons fenestrated in a manner similar to those of *T. loveridgii*, whilst one of 225 mm. has them thin but entire.

The ribs of the latter on the other hand, and seemingly the neural arch of the vertebræ, do absorb with growth; the ribs completely in most cases. Thus the bony plates are developing, whilst the ribs are degenerating by osteoclastic absorption—a process which is, of course, physiological, and in fact, as far as the ribs are concerned, carries to a logical conclusion a tendency which is well marked throughout the genus.

The question which now arises is: what has led to the extraordinary degree of depression of the carapace? Some individuals are positively concave above, and all have a markedly deformed and rickety appearance.

Flattening is evidently not brought about, at any rate to this extent, by a fenestrated or thin condition of the carapace, for the giant tortoises which pass through these stages in the course of development and have very thin carapaces, are remarkably convex in form. The only visible result here is the crumpled appearance of the shell of *T. abingdonii*. *T. polyphemus*, on the other hand, is distinctly flattened.

It can be argued on the one hand that the flattened carapace is brought about by the habit of living beneath stones and squeezing into rock-crevices. This habit, induced by environment, would be bound to have a modifying effect; for, during youth, the development of a domed and solid carapace would be interfered with by the constant application of pressure, and in a sufficient number of generations the ability to form a normal carapace might be lost altogether. The fact that the Burrowing Tortoise, *T. polyphemus*, has a thin or fenestrated and somewhat flattened carapace supports this view. Could this be proved experimentally, it would furnish a convincing argument in favour of the heritance of acquired characters.

On the other hand, it can be equally well maintained that an inherited tendency to the arrest in development is orthogenetic, brought about either gradually or as a mutation, and that the furtive habit of hiding beneath stones was the natural result, since the tortoise no longer possessed adequate protection from enemies.

Possibly both principles come into play, the reduced armour and loss of ribs being orthogenetic, and the depression and relative condition of the vertebræ being subsequently induced by the rock-dwelling habit.

Again, the metabolism of bone formation may be to some extent influenced by climatic conditions, lack of lime in the soil or water etc., or by their food. In this connection it is interesting to note that Mr. Loveridge has recently found two specimens of *Cinixys belliana* in the *T. loveridgii* locality which have remarkably depressed carapaces (31 °/₀ of total length as against over 40 °/₀); and, further, Tornier describes one from Bussisi, the *T. tornieri* locality, which has its bony plates excessively thin, and actually fenestrated. Possibly this individual, if let alone, might have founded a race of soft-shelled tortoises in this genus also.

The actual process of development of the bony plates of both carapace and plastron in *T. loveridgii* is really quite normal; in spite of the astounding appearance which they present in the adult, they are similar in general form to those of the young of other species. In some, of course, one set of elements may develop more quickly in proportion, altering the balance of the fenestræ or their outlines, but the same process is gone through by them all.

On dissecting a series of the young of *Testudo horsfieldii*, I find that the very young (50 mm.) presents a bony network of costal and neural plates, modified ribs, and undeveloped plastron, similar to the young *T. loveridgii* (60 mm.). The two are compared in text-fig. 21. Series in other species, chosen at random, show the same thing, with, of course, variations. In some the dermal plates are more equalized, and in the early stages present a less net-like form, each costal being kite-shaped, rather as in the Turtles. In the Giant Tortoise (*T. nigrita*) from the Galapagos, a very young specimen (95 mm.) has the bony carapace still extensively fenestrated; the costal plates are more or less equally developed, each being dilated beneath the vertebro-costal sutures, and from thence narrowing to the marginal region, the fenestræ between are therefore equal. The neural plates are broadly developed; second, fourth, and sixth are not in contact with the corresponding costals. The general structure is therefore in essentials the same as in *T. loveridgii*. In Freshwater Tortoises, such as *Emys*, development is proportionately quicker beneath the vertebral shields, a specimen of 50 mm. having this part of the carapace entire, whilst the costal region is only half completed.

In the following section the development of the costal and neural plates will be dealt with further, in connection with their origin.

Origin of the costal and neural plates.

Much has been written on the origin of these plates, and many ingenious theories have been propounded*.

Most authors agree that the marginals, nuchal, and pygals are of dermal origin, and that the plastron is derived from the sternum and gastralia which have become greatly modified, but the question of the neurals and costals is still unsettled.

The earliest opinion worth citing is that of Cuvier (1799), who considered that the costal plates were formed "par les dilatations de huit côtes ou bâtons osseux qui prennent naissance sur les unions des vertèbres, et se terminent à un rebord qui entourent toute la carapace." The idea that the plates are dilatations of the vertebral spinous processes and true ribs is held by many subsequent authors—Geoffroy St. Hilaire (1809), Bojanus (1819–21), Rathke (1848); or, further, that these plates originate in periosteal or differentiated tissue—Goette (1899), Haycraft (1899), Newman (1906). Haycraft (1891) formulates a theory that costal plates are rib-expansions formed where there is no differentiated periosteal membrane confining the rib. In the case of turtles, where the expansion does not reach the marginal, he states that the distal portions which preserve their rib-like form are unable to expand because "they are invested by a restraining periosteum." The fact that the costal plates in most Chelonians develop gradually towards the marginals, passing through the stage normal to adult turtles, disproves this theory.

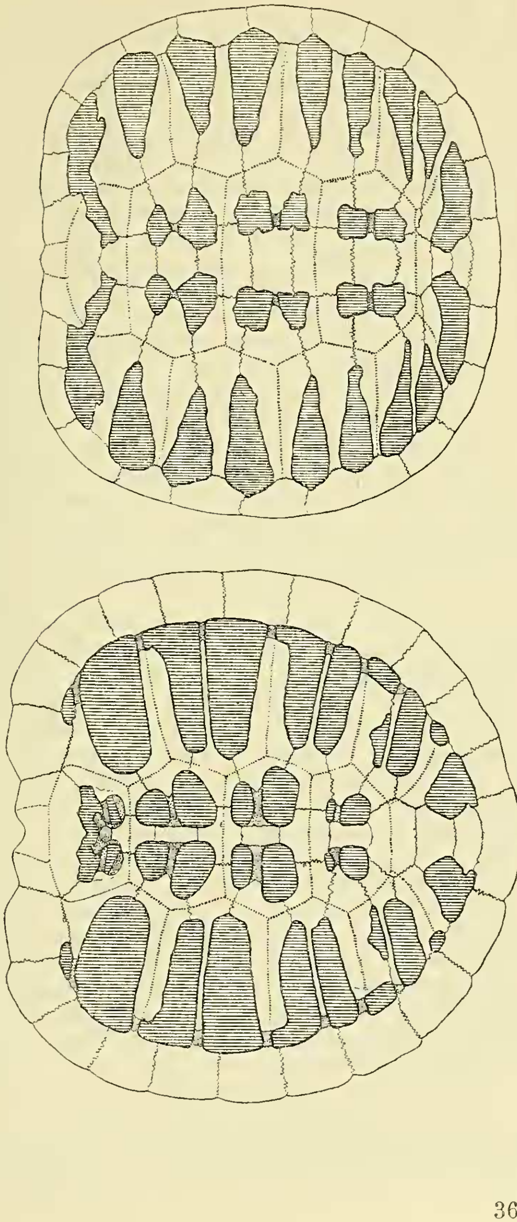
Carus (1827) and Gegenbaur (1889) thought that the costal plates were greatly developed vertebral transverse processes—a view which, of course, is immediately disproved by the fact that their points of origin are distinct and widely separated from the vertebral column.

O. P. Hay (1901) accepts none of the foregoing theories. He distinguishes three layers of bone—dermal, fascial, and cartilaginous. The first is present in the armour of *Dermochelys*, the most primitive living Chelonian. The modern costal and neural plates are formed not by dermal but by the fascial bone, which since it is completely united to the cartilage elements, appears to arise directly from the perichondrium, as observed by Goette (1899).

That these plates are dermal in origin and similar in every way to the nuchal, pygal, and marginal plates was first suggested by Carus (1834), and was followed up by Peters (1838), Owen (1849), Baur (1887), Gadow (1899, 1905, 1909), and Versluys (1914). Many points brought to light in the present study corroborate this view. For instance, the fact that the true ribs are degenerating throughout their length by absorption within the periosteum whilst the costal plates are in process of actual development, and also the marked difference in the texture of

* "Hypothesis follows hypothesis; the theoretical rubbish-heap accumulates; and truth ever eludes us."—Fabre (transl.).

Text-figure 21.



a b.

Young specimens of *T. loveridgii*, a, and *T. horsfeldii*, b, compared.
Epidermal shield-sutures ....; underlying rib :::::; fenestræ

the two forms of bone, seem to indicate that these are independent structures. It will also be remembered that in stripping the carapace from the young specimen of 42 mm., some of the neural plates adhered to the carapace rather than to the vertebra. Another point against endo-skeletal origin is the alternating level at which the costal plates arise on consecutive ribs, according to the arrangement of the epidermal shields above them.

This brings up the question, also unsettled, regarding the correlation of epidermal shields to the underlying plates. If the plates are of dermal or fascial (sub-dermal) origin, one presupposes such a correlation; if of endo-skeletal origin, there should be none. Various authors argue the case accordingly, H. H. Newman opposing any idea of correlation very strongly, whilst Gadow treats it as an accepted fact. G. H. Parker (1901), in his paper on the Sculptured Tortoise, attempts to explain the alternating arrangement of these two structures by applying Harrison's observations on the regenerating tail of a tadpole (1899). He says (p. 23):—"The tail of a developing tadpole is composed of an outer covering of ectoderm—which ultimately gives rise to the outer layers of the skin—and of a core of mesoderm. These two masses of tissue grow in very different ways, so that as the tail lengthens, the ectodermic covering, which is most actively produced anteriorly, slips posteriorly over the underlying mesoderm, whose region of growth is chiefly at the posterior end. Although this posterior migration of the ectoderm has been actually demonstrated only in the tadpole, there is reason to believe that it occurs in other vertebrates."

The present study points to a very marked and obvious correlation between shields and plates in *Testudo loveridgii*, which, having its carapace in what one might term an incipient stage of development, throws much light on the subject. A careful study of many species of *Testudo* and *Cinixys* during the period when the plates are developing, brings forth a wealth of evidence that this correlation is an indisputable fact in these genera. In newly-hatched individuals of *T. loveridgii* (and also those of *T. ibera*, *græca*, *horsfieldii*, *leithii*, etc., etc.) the bony plates are lacking beneath the areolars, developing apparently as the shields themselves commence to form their growth-rings. In specimens of different species the amount of plate which has accrued at the end of the season's growth varies, but is at first in all cases greater beneath shield-sutures (that is around the shield-edges) than elsewhere. The neural plates beneath a shield-suture are developed laterally, whilst the alternating ones are not. The costal plates beneath the costal shield-sutures are at least twice as broadly developed as those between; their proximal portions, however, alternate in breadth and narrowness inversely in strict accordance with the overlying shield-sutures. Moreover, in the male type-specimen the X-ray plate (*vide* Pl. III.) shows that the bony plates are in perfect harmony with the abnormal third vertebral shield-sutures, and are thus adapted to support four instead of five vertebrals. This fact points to dermal origin of the plates, but is in opposition to Parker's theory of ectodermic migration in Chelonia (*à propos* of the tadpole's tail), in which he points out that "any early local disturbing influence that affected both scute- and plate-producing tissues would leave its trace in the adult in the form of a region of modified scutes posterior to a region of modified bony plates." At the same time, this does not alter the fact that the plates are adherent to the bones of the true skeleton, and are coincident with them regarding numbers etc. Yet development seems to be influenced and regulated chiefly by that of the overlying dermal areas corresponding to the epidermal shields. This is also seen in the Giant Tortoises known to have thin carapaces, such as *T. abingdonii*, *microphyes*, etc., in *T. calcaratus*, and in fossil forms such as the Pleistocene Marsh Tortoises, *T. vosmaeri* from Rodriguez and *T. indica* from Mauritius. In these the form of the plates is similar to that of *T. loveridgii, the essential network beneath the shield-sutures being of thick bone standing out in relief from the thin bone, which fills in what would be fenestræ in the young or in* loveridgii.

In ordinary adult tortoises in which the carapace is complete and of equal thickness, this cannot be appreciated, but in these it can be studied in the initial stages of plate-development.

The following quotation from Owen (1849, p. 161), whose paper I had not read at the time of my own observations, corroborates in every particular what I have found to be the case in so many species:—

"A strong argument for regarding the costal plates as dermal ossifications rather than processes or continuations of the endoskeletal elements, to which they are attached, may be drawn . . . . from the period of their ossification, and their relative position to the ribs with which they are connate.

"In the embryo *Testudo indica** the uniformly slender pleurapophyses are ossified nearly throughout their whole length before the ossification of the costal plates, usually regarded as their expanded tubercle, commences; and the beginning of the superadded bone † is not at the same point in each rib, as might have been expected if it were the exogenous process called 'tubercle' of the rib. The costal plates are situated in the young *Testudo indica* alternately nearer to and farther from the head of the rib; and their presence seems to be determined rather by the angle of union of the superincumbent vertebral scutella with the lateral or costal scutella, than by the necessity for additional strength of the articulation of the ribs with the spine. Ossification commences at the point from which the three impressions radiate, and as this point is

* [Probably *T. nigrita* or *elephantina*, *indica* Schn. being an extinct species.]

† "This period, in its relation to the development of the neural arches and pleurapophyses, corresponds precisely with that at which the dermal plates of the Crocodile begin to be ossified."

nearer the median line at the median apex of the costal scutellum than at the lateral apex of the vertebral scutellum, the resulting plates of bone are alternately further from or nearer to the middle line; and the first, third, and fifth costal plates have advanced along the proximal end of the rib so as to join the neural plates, whilst the second, fourth, and sixth costal plates leave a portion of the proximal end of the rib uncovered and crossing the space between the incipient costal plates and the neural plate. . . . .

"When the partially ossified carapace of a young tortoise is dried, one cannot fail to be struck with the difference in the texture and external surface of the bones which unquestionably belong to the endo-skeletal vertebræ, and of those which, notwithstanding their connection with neural spines and pleurapophyses, are developed in the fibrous substance of the corium. These nascent 'neural' and 'costal plates' of the carapace have a granular exterior and a coarse spongy texture, whilst the neural arches and pleurapophyses are compact, smooth, and with a polished external surface: the part of the pleurapophyses which passes beneath and is attached to the under surface of the 'costal' plate (pls. i.–viii.), contrasts strikingly with that superimposed dermal ossification.

"The marginal plates present the same rough, coarse, granular character as the neural and costal plates . . . . . their ossification has been governed by the presence of the marginal epidermal scutes, and, as in the case of the costal plates, by the points of junction of contiguous scutes; each marginal ossification is accordingly impressed by the lines indicating the junction of the marginal epidermal scutes with each other and, in the case of the middle ones, with the contiguous scutes of the plastron."

The whole of the foregoing evidence therefore points to the fact that the costal and neural plates are of dermal origin, not endo-skeletal; and are, in fact, similar in this respect to the nuchal, pygal, and marginal plates.

Further, the corrrelation between the epidermal shield-sutures and the plates beneath, observed independently in the present study and previously by Owen, suggests that their growth is also correlated.

The areas of dermis beneath each shield are well marked off from one another by a fold and an underlying groove in which the shield-edges are implanted. It is probable that these dermal areas grow in the same manner as their superimposed shields, and that the bony plates beneath, which are of dermal origin, have their growth similarly regulated.

The following hypothesis is therefore suggested :—

That the bony plates of the carapace develop from the dermis, primarily in the areas of growth activity.

(*a*) Where this takes place concentrically, as seen by such striations in the epidermal shields, the plates in the early stages of development are localised principally beneath the shield-sutures, as in *Testudo*, *Cinixys*, etc.

(*b*) Where growth is uniform throughout each area, development of the plates is also equalised, proceeding from the individual centres of ossification, as in *Emys* etc.

Summary.

Testudo loveridgii has an excessively depressed soft-shelled carapace, and is able to inflate itself to a certain degree. It possesses a bony carapace and plastron, but they are extensively fenestrated, incomplete, and similar in essentials to the juvenile stages of other species.

Marginal plates five, six, and seven spread inwards in a unique manner, entering into the composition of the plastron and separating the hyo- and hypoplastrons from each other. Their upper portions are extraordinarily shallow.

The ribs in *T. loveridgii* become (usually) entirely absorbed, apparently by the osteoclasts which are present beneath the periosteum. A simulacrum of the capitular portion, soft like ligament, and formed chiefly of periosteum, persists for some while.

The neural arch is vestigial and sometimes completely wanting, the neural plates being applied to the depressed centra to form the roof of the neural canal. Absorption probably takes place to some extent as in the ribs, but the arch is never more than a simple layer of bone, without spinous processes.

The jaws, together with their investing horny sheaths, are denticulated with remarkable regularity.

Fenestration in this and other species is caused by arrested development, and not, as previously supposed, by absorption with age.

The development of the bony plates in T. loveridgii and the young of other species *points to the neurals and costals being of dermal origin.* The principal evidence is :—

(1) *That they are developing whilst the ribs and neural arches of the true skeleton are degenerating.* (2) *That the point of origin of each costal plate is alternately nearer to and further from the rib capitulum.* (3) *That the form of these plates in their early stages of development is in strict correlation with the borders of, or sutures between, the superincumbent epidermal shields.*

It seems possible that *the development of the plates is regulated by that of the areas of dermis corresponding to the epidermal shields ;* (1) *forming a network as in* T. loveridgii *and other species when this growth proceeds concentrically*, or (2) *proceeding equally from each centre of origin where dermal growth takes place equally within each area as in* Emys *etc.*

Notes.

The following field-notes and observations on the original specimens, and those collected on subsequent expeditions, are contributed by Mr. Loveridge:—

"*Habitat.*

"The first specimen of this tortoise which I met with was found dead at the foot of a precipitous rock some 40 feet in height and situated near the top of a rocky kopje 500 feet above the surrounding dry thorn-bush country. From the flattened and broken remains, I concluded that it was a species unknown to me, and crushed by a rock having fallen upon it. (The rocks are grey granite, sheer precipices on the kopjes and rounded boulders scattered on the plains around. Most of the specimens have been collected beneath the latter.) On December 8th, 1918, my native collector brought in a small specimen which I at once assumed was *T. tornieri* Sieb., of which I had read brief notices but had never seen the original description. During succeeding days two batches of these tortoises were found in crevices or beneath rocks, but though I did not leave the district till December 28th, and had a native looking for them constantly, no more were found.

"On January 1st, 1921, I sent the same boy who was with me for two years before, back to the same locality which lies south of Dodoma in arid country. Here, again, he found but two or three specimens, but, ranging round, came upon another kopje where they were more plentiful, though he alleged that without a single exception they were under the rocks, of which he had to remove a great many before being able to effect captures. He had one piece of good fortune in finding four young specimens all together beneath one boulder, with the exception of a slightly larger one already caught; these were the only young specimens taken. The smallest of these was unfortunately trodden upon and promptly died. The shell is much depressed as in the adult. When Mr. Boulenger described the species in 1920, he assumed a small dome-shaped tortoise, which I found preserved in a bottle (no data) in a German house near Morogoro, to be the young of *T. loveridgii*; this, however, is disproved by the finding of young specimens with depressed shells.

"In November 1921, I spent an afternoon with my boy looking for *T. loveridgii* at Dodoma. He first took me to the place where he got the eleven tortoises, which is not on a kopje but on a huge rock 100 yards from a kopje. The rock is about 30 feet long and 10 feet wide, and slopes up from the ground to a height of 7 or 8 feet. On the knob is a flattish boulder, and beneath this he found them all in January (evidently æstivating—January and February being our hottest months). The tortoises therefore climbed up the boulder: one would certainly never think of looking for them in such a spot. We then went to the place where he found the three—in a cleft of a split boulder; they had to climb the boulder and slide down an almost vertical cleft, where one would suppose they could not get out; the cleft was about 18 inches. In this cleft, amongst a litter of dead leaves, were two not half-grown individuals. We hunted about all the rest of the day, but found no more. . . . Their markings are very fine; Tabora specimens are noticeably darker than the Dodoma ones.

"*Pairing.*

"On December 12th, 1921, at 4.30 P.M., I observed two specimens paired for the first time. A native said they had been so approximately for half-an-hour. The shell of the male formed an angle of 45° with that of the female; his fore-feet were in the air; he kept moving his head in and out of his shell and had his mouth wide open. In April this female and others were heavy with eggs. On January 13th two more tortoises were paired at 9 or 10 A.M. and from that date and onwards pairing took place daily, usually between 9 or 10 A.M. and 2 P.M. The female generally walked away with the male following; frequently the latter became impatient and snapped at her limbs, or crawled on her back, making vicious snaps at her head whenever it appeared. On a couple of occasions the males were so ill-tempered that they seized the edges of the females' shells in their jaws and dragged them along, finally getting beneath them and apparently endeavouring to overturn them.

"*Habits of* T. loveridgii *compared with those of* Cinixys belliana.

"As I had these species under observation for four months confined in the same enclosure, I found it very interesting to compare the habits of an exceptionally highly-specialised Box Tortoise with those of a retrogressive and soft-shelled species.

"Owing to neither my native collector nor myself finding *T. loveridgii* in the open, I had come to the conclusion that it was nocturnal; with a view definitely to ascertain if this were indeed so, I visited the enclosure at all hours of the night up to 1 A.M., but with one or two solitary exceptions never found them out. At dusk they always retired beneath the heaps of stones and boulders provided for them, and there they piled themselves up, one atop of another, a great deal of noise being caused by the scratching of claws on shells. They did not again make an appearance until several hours after daybreak, which varied according to the dullness or brightness of the morning.

"*C. belliana*, on the other hand, not infrequently stayed out at night, and particularly when rainy; all seven of them would spend the night in trying to escape from the enclosure. Moreover, *C. belliana* was always on the move at daybreak. On further reflection it was obvious that in their soft shells *T. loveridgii* would fall an easy prey to the carnivores roaming about after nightfall, and which are very plentiful in the Dodoma district

(Leopard, Ratel, Civet, Mungoose). This was brought home to me very forcibly one night by a Civet entering an adjoining enclosure and eating four and a half young crocodiles in one night. The shell of *C. belliana* would resist most attacks; the thickness of their bony defence as seen in a sawn-through section is astonishing.

" *T. loveridgii* shows a fondness for climbing up and falling off the rockeries of its enclosure, which pastime, indulged in in its natural habitat, calls for a rapid recovery in turning over; it also displays great agility in climbing up wire netting. One day eight specimens of the Soft Tortoise succeeded in escaping through a hole in the wire netting; two were recovered in three days, being found on the second and third days at some huts 400 yards from the hill. They appear to feed oftener than *C. belliana* and are quite voracious. They feed well on a succulent grass here; the previous specimens taken home were fed on lettuce, and when this failed were induced to eat bread soaked in jam. *T. loveridgii* generally retires to its retreat when a shower comes on, but on occasion I have known the whole lot turn out during heavy rain and feed voraciously, probably being thirsty.

" I was at first disposed to think that *T. loveridgii* could not swim, as the first half-dozen arrivals on being placed in water sank to the bottom of the bath and remained there without putting forth any effort. On seeing some young ones struggling in water and trying to swim, I retried a couple of females, which struck out well and kept themselves up when placed in a bowl of water."

Unfortunately nearly half of these valuable tortoises, kept alive by Mr. Loveridge, succeeded in escaping, several doing so *en route* to the coast on their way to me. Several spirit specimens also came to grief, but a sufficient number remain, reinforced by still later collections, including a beautiful series of young, to enable a thorough study of this most variable species to be made.

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EXPLANATION OF THE PLATES.

PLATE I. *Testudo loveridgii* Blgr. (¾ nat. size).

PLATE II. Radiograph of ♀ type-specimen (nat. size). Showing correlation between bony plates and epidermal shield-sutures (visible as a network of white lines).

PLATE III. Radiograph of ♂ type-specimen (nat. size). Showing correlated shield and plate abnormalities.